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Morphological observations on a hatchling and a paralarva of the vampire squid, *Vampyroteuthis infernalis* Chun (Mollusca: Cephalopoda)

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Abstract.—We present morphological observations on two very small vampire squids. One, a trawl-caught hatchling of 8 mm mantle length (ML), had embryonic features including internal yolk, broad arm-like filaments, and lack of mantle-head fusion. The other was a 9 mm ML paralarva collected by submersible and photographed alive aboard ship. Although only slightly larger than the hatchling, its morphology was much more like that of larger specimens than that of the hatchling, except for the oblique orientation of its fins.

The vampire squid, *Vampyroteuthis infernalis* Chun, 1903, is the only living member of the Vampyromorpha, the sister group to the Octopoda (Young & Vecchione 1996, Young et al. 1998). Through outgroup and ontogenetic comparisons, this species holds important clues to our understanding of cephalopod evolution and to the reconstruction of ancestral character states. Very little has been published, however, concerning its anatomy, behavior or embryology. As a result, any new information is valuable. We report here on two very small vampire squid. One, a hatchling captured by trawl, was dead but in excellent condition when retrieved. The other was a paralarva (= "stage 1 larva", Pickford 1949a) captured alive from a submersible and photographed in a shipboard aquarium. These are the first observations of a live vampire squid paralarva. Together, these observations support many morphological characters described by Pickford (1949a) from damaged specimens.

Materials and Methods

The hatchling *Vampyroteuthis* (8 mm ML, USNM 885891) was captured near the Hawaiian Islands on a cruise of the R/V *New Horizon* off leeward Oahu on 1 July 1996. The collecting gear was an opening–closing net that fished between 0130 and 0743 h at a depth of about 1050–1300 m (Sta. 62). The specimen was sorted from the catch soon after collection, and photographs were taken aboard ship shortly thereafter. The paralarva (9 mm ML, USNM 816886) was captured in the eastern Gulf of Mexico using a pelagic suction sampler from the manned submersible *Johnson Sea Link II* during dive 1453, 30 August 1987, 24°30′5″N, 83°45′12″W at 830 m depth. It was photographed while still alive immediately after the submersible returned to its support ship.

Observations

Hatchling.—The trawl-caught animal was clearly a hatchling (i.e., there was no chorion surrounding it), but morphologically it was an advanced embryo presumably incapable of feeding except from its internal yolk supply. A large mass of yolk globules, presumably within a large internal yolk sac, was seen through the transparent gladius ventral and lateral to the esophagus.

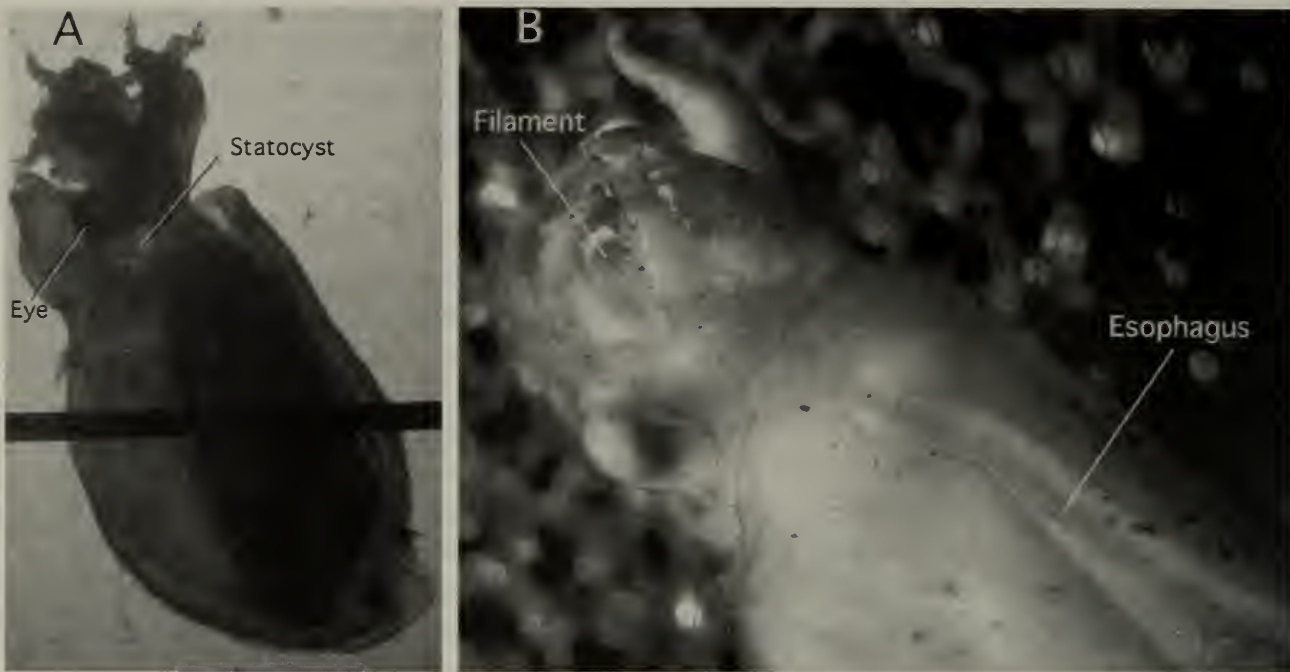

Fig. 1. Photographs of freshly collected *Vampyroteuthis infernalis* hatchling (8 mm ML). A, Lateral view with dissecting pin laying across mantle to prevent motion from the ship's rolling; B, Dorsolateral closeup of head and anterior mantle.

During attempts to photograph the embryo aboard ship, a pin was placed on top of the mantle to keep the animal from rolling (Fig. 1A). This resulted in a sausage-shaped extrusion of yolk from the buccal region.

The body of the hatchling was very large relative to the head and arms (compare Fig. 1A with Fig. 3), the eyes were very small and the mantle was not fused to the head in the nuchal region (Fig. 2). The eye fold formed a circular fold around the base of each eye, not yet enclosing the eye. Although squid eyes often are forced out through circular eyelids during capture, this

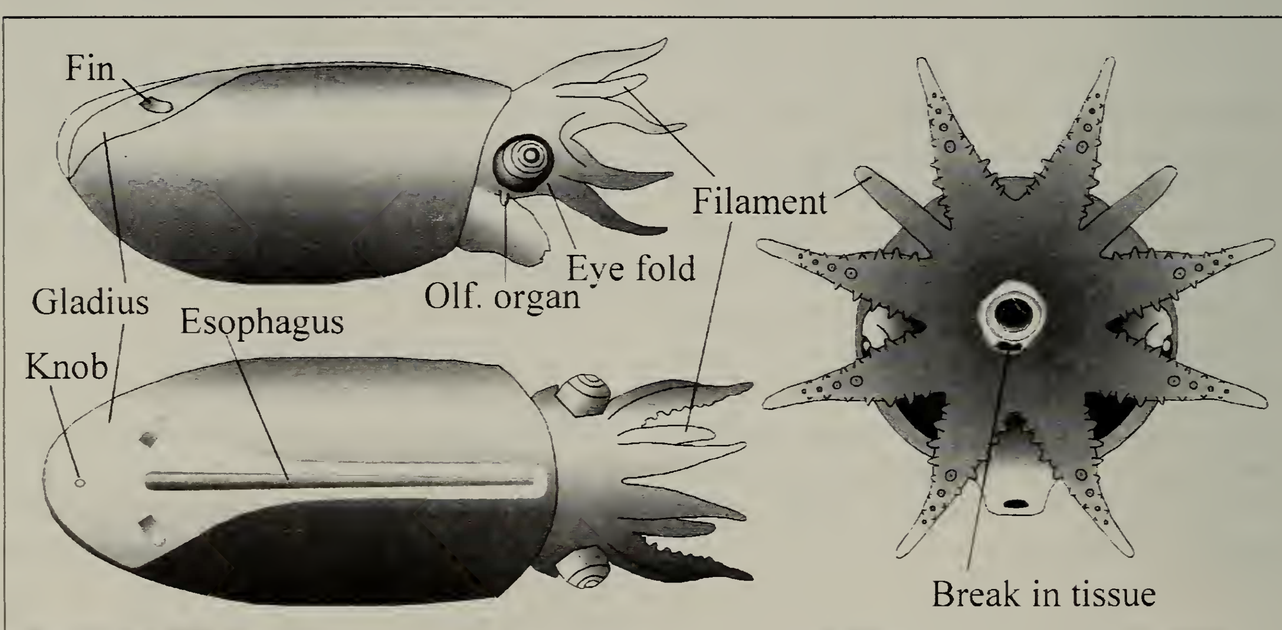

Fig. 2. Schematic drawings of *Vampyroteuthis infernalis* hatchling, lateral, dorsal, and oral views. From top to bottom on the oral view the arm pairs are dorsal (Arms I), filaments (Arms II), dorsolateral (Arms III), ventrolateral (Arms IV), and ventral (Arms V).

was not a case in this instance. The epithelial body could clearly be seen surrounding the lens of the eye even though the lens was partially covered by the iris.

Gelatinous tissue surrounded the arms and separated muscle layers in the mantle but did not cover the mantle muscle externally. At the posterior dorsal apex of the mantle a small knob (ca. 15 μm) was present in the epithelium and partially surrounded by a groove. This knob is in the position of the hatching organ of other cephalopods but we find it reminiscent of the peculiar circular feature in the photos of the paralarva (Fig. 3B–D) described below.

The filaments (= "velar filaments", Hochberg & Nixon 1992) were intact. Each was broad, short, of uniform thickness to the rounded tips (Figs. 1B, 2), and lacked both suckers and cirri. Their attachment to the brachial crown was as in the adult except that the filaments did not reside in a pocket, as a web was virtually absent. A slight ridge between arms III, IV and V (Fig. 2) appeared to be the web precursor. The arm tips were slightly damaged but all seemed to be subequal and armed with cirri and suckers. Four developing suckers were counted on one arm and we assume this to apply to all arms. Suckers had constricted bases but lacked obvious stalks. Four pairs of cirri preceded the first sucker and the suckers and cirri alternated as in the adult.

On the oral surface of the brachial crown, two circular lips and a more distal fold surrounded the beak. A break in the tissue ventral to the lips and medial to this fold was presumably the point where yolk came out. Unlike in adults, the large funnel was not embedded in the head, but no free adductor muscles were present. The exact orientation of the very small, but damaged, fins could not be determined. The pigmented esophagus, where it emerged from the brain, was clearly visible through the transparent gladius. The esophagus gradually increased in diameter posteriorly. The gladius was the same general shape as in adults but had a somewhat narrower median field.

The animal's coloration was faint pink-brown and fairly translucent. Black chromatophores were scattered at several points on the animal, especially on the oral surface of the arm bases and anterodorsally on the eye. A light reddish-brown epidermal pigment was present. The pigment was most obvious on the covering of the visceral mass, the ventral surface of the head and the oral surfaces of the arms. The animal seemed to be neutrally buoyant although small bubbles attached to the epidermis prevented actual determination.

Paralarva.—While nearly the same size (9 vs. 8 mm ML), the morphology of the paralarva was very different from that of the hatchling. Except as noted below, the overall appearance was similar to that of larger juveniles and adults (e.g., head/mantle fusion, pigmentation, etc.). The oblique angle of the fin noted by Pickford (1949a) is confirmed here in photographs (Fig. 3B, C) of the living paralarva. The fins were the first of two pairs to develop (= "juvenile fins" or "larval fins", Young & Vecchione 1996); the second pair ("adult fins" Ibid) were present only as minute precursors anterior to the fin-base photophore. Also apparent in these live photos (Fig. 3B–D) is a peculiar circular feature at the apex of the mantle. Examination of the preserved specimen, however, revealed no obvious structure at this location. Figure 3A shows the arms in a forward orientation, and Fig. 3B shows them in the lateral orientation. The filaments were very thin and emerged from pockets in the well-developed web, as in older specimens. The incompletely retracted but coiled filaments are seen most clearly in Fig. 3C. The eyes of this young vampire squid were relatively small (Fig. 3A, C), compared with those of an adult.

Discussion

Pickford (1949a) described a young vampire squid in the same stage of development as the hatchling described here. However, her specimen was badly damaged (mantle

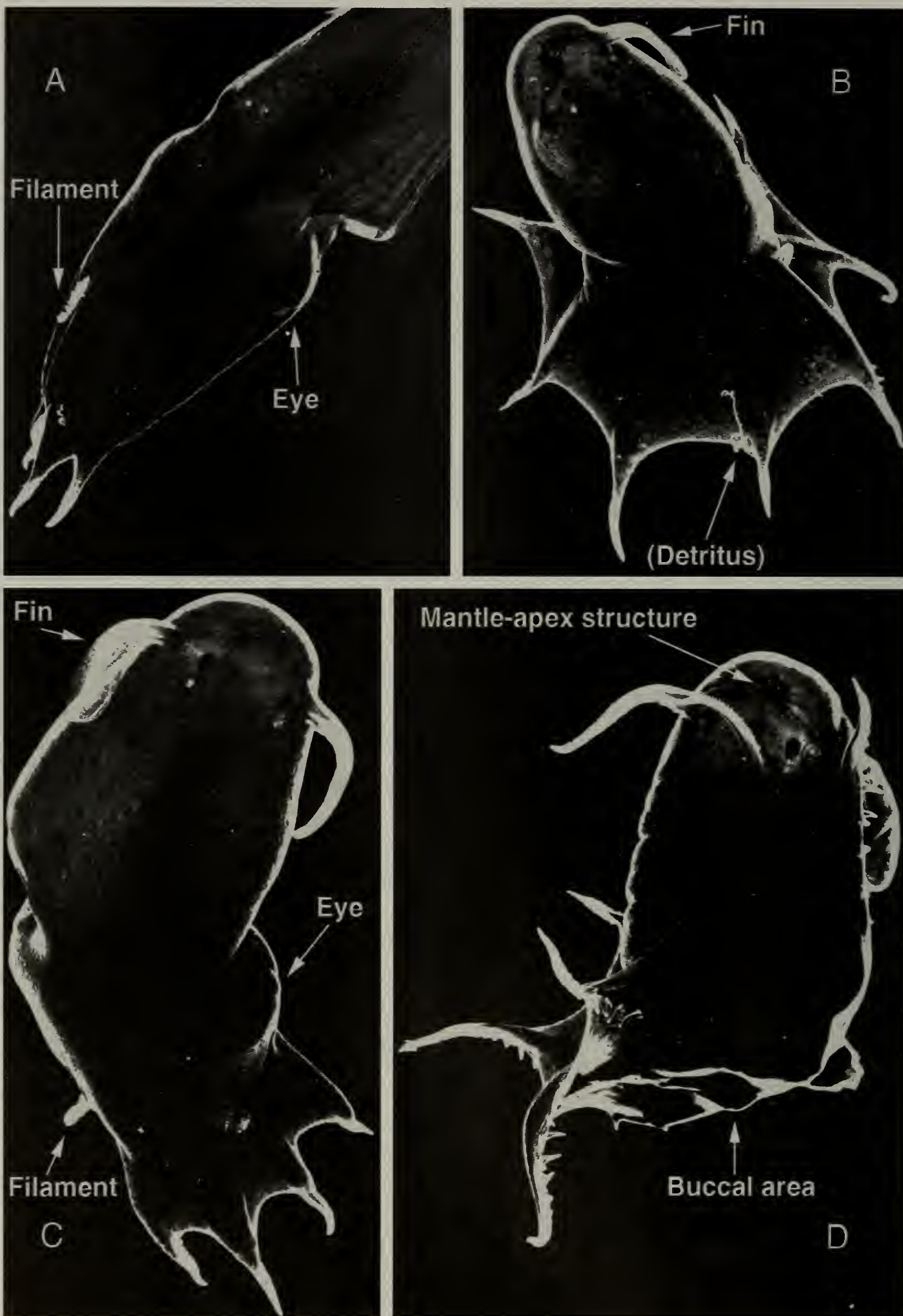

Fig. 3. Photographs of live paralarval *Vampyroteuthis infernalis* (9 mm ML). All views dorsal. A, with arms in anterior orientation; B, with arms and web spread laterally; C, showing coiled, partially retracted filament; D, with arms and web folded posteriorly revealing buccal area.

length was thought to be 5.7 mm) and, as a result, some of her conclusions have been in doubt. The description here confirms some of her more important findings (e.g., mantle free from head; thick filaments).

The vampire hatchling also confirms the fusion of the head and mantle in octopods and vampyromorphs to be independent, as predicted from morphology (Young & Vecchione 1996). The broad filaments are more arm-like than in older vampire squids and add support to the interpretation that the filaments are the second pair of arms. If they were ocular filaments, as suggested by Young (1967), one might expect that they would be especially small at this stage. The embryonic eye fold in cephalopods is continuous with the arm bases and the particular arms associated with the fold have been used to determine the homology of arm pairs in decapods and octopods (Boletzky 1993). Unfortunately, in the vampire hatchling the eye fold does not continue onto the arm crown, presumably because of its advanced stage of development. A fold surrounding the lips could be the remnant of a buccal crown that is otherwise absent in *Vampyroteuthis* (see Fig. 3D). More likely, however, this is the demarcation between the gelatinous tissue and the more muscular region where the arm muscles fuse with one another and has no phylogenetic significance.

Vampire hatchlings may drift freely in deep water until they change into the form of a typical paralarva. However, the specimen examined here could be an advanced embryo, hatched prematurely within the trawl. Pickford (1949b) stated that the egg size of spawned *Vampyroteuthis* eggs is up to 4.0 mm in diameter. Clearly the present hatchling with its embryonic features (e.g., yolk) was not derived from such a small egg. An egg size of ca. 8 mm (i.e., comparable to the mantle length) would be expected. The discrepancy cannot be explained at present.

Young et al. (1998) proposed that relaxed orientation of the arms in *Vampyroteuthis* might provide evidence to choose between alternative hypotheses about octopodiform evolution. However, the photographs of the paralarva with its arms both spread laterally and projecting anteriorly are equivocal on this question.

Vampyroteuthis infernalis currently is considered to comprise a single panmixic species. Therefore, although our specimens were collected in different oceans, we do not believe that the morphological differences between them reflect interspecific variability. The strong differences in morphology between our two specimens, which are nearly the same size, demonstrate the changes that occur in the early post-hatching ontogeny of *Vampyroteuthis.* Pickford (1949a) described the paralarval development of *V. infernalis.* One peculiarity of this species is that early paralarvae (Pickford's "stage 1 larvae" have one pair of fins; then a second pair develops ("stage 2") followed by absorption of the original pair ("stages 3 and 4"). She observed that the fins of the paralarva are set obliquely on the body, unlike the horizontal attachment of the adult fin, and suggested that the young vampire hangs head downward in the water. The present observations, which are the first live of a paralarval vampire squid, confirm Pickford's descriptions, such as fin orientation, which were based on preserved specimens.

The pucker-like circular structure seen near the posterior apex of the paralarva's mantle is similar to that recorded in a subadult *Vampyroteuthis* videotaped as part of a televison program about cephalopods ("Incredible Suckers"). No discrete structure is apparent on the preserved paralarva and we do not know the function of the structure.

Acknowledgments

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